THE EARLY DEVELOPMENT OF THE LATERAL LINE SYSTEM OF AMIA CALVA.[1]

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The earliest stage of the lateral line system of *Amia* described by Allis ('88) is in an embryo a day after hatching. In this stage the supra-orbital, infra-orbital, opercular-mandibular and the post-auditory lines are well formed but no individual sense organs are differentiated. Wilson ('91) has described for *Serranus* a common anlage for the lateral line, auditory organ and branchial sense organ. An elongated furrow formed from the inner layer of the ectoderm lies on either side of the neural tube. This furrow becomes divided by transverse constrictions into anterior, middle and posterior parts. The anterior and middle parts are transformed into vesicles by the closing together of the lips of the furrow and become respectively the branchial sense organ and the auditory organ. The posterior part remains as a groove and is converted into the lateral line.

Wilson and Mattock ('97) describe for the salmon a thickening in the form of a solid cord which behaves exactly as the furrow in *Serranus*. It is constricted into three parts, the two anterior of which form vesicles, while the posterior remains as a cord which is the anlage of the lateral line. Mitrophanow ('93) has described a similar condition in selachians. In this case there is a shallow furrow which merges gradually into the surrounding tissue, thus giving a less distinctly defined groove than in *Serranus*.

The present work was begun with the purpose of tracing the lateral line system in *Amia* from its first appearance up to the point where Allis took it up (*i. e.*, in embryos a day after hatching). It was thought possible that the anlage was formed and differentiated in *Amia* as described for teleosts by Wilson and Mitrophanow. The work was done at the Zoölogical Laboratory of the University of Michigan in 1900, under the direction of Professor Jacob Reighard, to whom I wish to express my sincere thanks.

[1] Contributions from the Zoölogical Laboratory of the University of Michigan, No. 114.

In embryos in which the optic vesicles and hind brain are just being differentiated from the neural tube there is seen in surface view a thickening (Fig. 1, *th.*) on the neural tube just back of the hind brain. This thickening appears to be a lateral extension of either side of the neural tube and is very similar in appearance to the optic vesicles. It was thought that this might be the anlage for the lateral line. This view was made more probable by the fact that in a later stage (Fig. 3, *th.*), when the first gill slit (spiracular) is formed, this thickening becomes divided on either side by a transverse fissure into two lobes, the cranial one of which lies opposite the hyoid arch. This bilobed condition suggests the division spoken of by Wilson in teleosts.

Sections (Fig. 2, *n.c.*) through the region of this thickening in the first stage described (*i. e.*, Fig. 1) show the neural tube still connected with the ectoderm while a wedge-shaped mass of closely packed cells, or neural crest, lies on either side of the tube between the ectoderm and the dorsal surface of the tube. Laterally these wedge-shaped masses project out beyond the neural tube. The lines of separation between this very much thickened neural crest and the neural tube on one hand and the ectoderm on the other are very indistinct. This neural crest corresponds exactly in position and extent to the external thickening described for the stage shown in Fig. 1.

In sections through the anterior half there is on either side of the crest the deep auditory invagination of the inner layer of ectoderm. The invagination is directed ventrally and inward toward the neural tube. The medial side lies against the broad end of the wedge-shaped neural crest. The wall of the auditory invagination consists of a single layer of columnar cells. The two walls are separated from each other by a plane extending from the outer layer of ectoderm to the inner surface of the invagination (Fig. 2, *a.in.*). Sections toward the anterior end and middle of the crest show that the auditory invagination ends abruptly in both cranially and caudally.

In a little older embryo (Fig. 3) sections show that the neural tube has lost its connection with the ectoderm. The neural crest has become divided into an anterior and posterior lobe as described in surface view and is not so clearly defined as in the pre-

vious stage, since the cells are more loosely packed and the cells of the ventral and lateral surfaces merge gradually into the surrounding mesoblast (Fig. 4, *n.c.*). On account of this pushing apart of the cells the crest extends farther ventrally along the sides of the neural tube. Laterally it extends out on either side to a distance equal to the width of the neural tube. The auditory invagination lies between the two lobes of the crest. A cavity has appeared in the auditory invagination in the form of a slit separating the two walls along the plane spoken of in the previous stage. A constriction separating the invagination from the ectoderm is in process of formation.

In a stage in which two gill slits (spiracular and first post-hyoidean) are formed (Fig. 5) the two lobes of the neural crest seen in surface view of the previous stage are no longer apparent in surface view. Sections show that the lobes of the neural crest have extended further laterally and at the same time thinned out dorso-ventrally so that they are transformed into two narrow bands of mesoblast extending outward and forward from the neural tube, one into the hyoid arch and the other into the first branchial arch. The auditory invagination lies at the median end of the post-hyoidean slit between the ends of the hyoid and branchial arches and extending into the mesoblast of the posterior edge of the hyoid arch. The constriction observed in the last stage between the ectoderm and the auditory invagination has proceeded until the auditory invagination is now a closed vesicle nearly separated from the ectoderm (Figs. 5, *a.p.*; 6, *a.in.*).

This auditory invagination was traced in sections of later stages until in a stage like Fig. 7 it has become a large vesicle, circular in section, lying some distance below the ectoderm. Its median half is partly covered by the hind brain so that only the lateral portion is visible in surface view. Its wall is composed of a single layer of cells which are more columnar on the median side than on the lateral.

The thickening on the neural tube proves then to be a mass of mes-ectoblast in the form of a neural crest in which the auditory invagination lies and so cannot be the anlage of the lateral line system. The neural crest of this region divides into two lobes which go in large part to form the mesodermal portion of the

hyoidean and the first branchial arches. It also probably gives rise to the seventh and ninth cranial nerves. In the region of the cranio-lateral portion of the neural crest there is on each side the auditory invagination of the ectoderm. This becomes constricted from the ectoderm and forms a closed vesicle or auditory vesicle. As the auditory vesicle undergoes no further division it is evident that the lateral line anlage does not arise in connection with the auditory organ as described in teleosts. The beginning of the lateral line system appears in a later stage.

The first indication of a lateral line is found in sections of a stage long after the establishment of the auditory vesicle (Fig. 7) and about a day and a half older than the stage represented by Fig. 5. A thickening of the inner layer of ectoblast caused by the cells becoming columnar runs along each side of the embryo in the angle which the embryo makes with the yolk (Fig. 8, *p.a.l.l.*). It extends from the second gill slit to the region of the first somite. It is not visible in surface view. This proves to be the anlage of the post-auditory division of the lateral line system.

In embryos about a day and a half older than that last described the lateral line is first seen in surface view (Fig. 9, *p.a.l.l.*). The post-auditory anlage has elongated so as to extend to the middle of the second post-auditory somite. It is a very slender cord formed from the ectodermal thickening described in the previous stage. It is of greater depth than in the earlier stages, so that its outer surface is slightly raised above the surface of the body. The anlage of the head lines also appear in this stage (Fig. 9, *s.o.l.l.*, *i.o.l.l.*, *o.m.l.l.*). The supra-orbital and the opercular-mandibular lines form a V, the arms of which extend craniad from a point just in front of the auditory organ. The supra-orbital extends to the caudo-dorsal portion of the eye and consists of two elongated bead-like thickenings end to end. The opercular-mandibular extends down the cranial edge of the gill cover and is a very slender line. Passing from the caudo-ventral portion of the eye and into the angle of the V is the infra-orbital line which is a short broad thickening. The lines in the head region are formed by thickenings of the ectoblast which project inward very slightly, but also raise the surface in the form of ridges. The thickenings are caused here also by the ectoderm cells becoming columnar (Fig. 10, *i.o.* and *s.o.l.l.*).

In an embryo that has just hatched (Fig. 11) the supra-orbital line extends cranially to a point just dorsal to the eye and is a continuous cord instead of being beaded. The infra-orbital line extends below the eye to the ventral surface of the nasal pit. The opercular-mandibular has changed but little from the condition in the previous stage. The post-auditory line has grown craniad so that the anterior end extends to about the middle of the auditory pit. Caudally it extends to a point half way between the operculum and the pectoral fin. This line consists in this stage of three elongated bead-like thickenings placed end to end.

The connection of the post-auditory line with the infraorbital line shows first in an embryo a day after hatching (Fig. 12). This is the stage with which Allis begins his description. The post-auditory line extends caudally to the pectoral fin and shows a fine beaded appearance. The head lines are very much broader than before and the supra-orbital extends farther over the eye. The infra-orbital sends a small twig up over the nasal pit. The line connecting the infra-orbital with the post-auditory line is a very fine cord. A very small twig is given off from this line just below the auditory organ and projects half way up the caudal border of this organ. There is no differentiation of the lines into definite sense organs in this stage.

Summary.

1. In very young embryos there is present a thickening on the neural tube which consists of a mass of mes-ectoblast of neural crest origin. In this the auditory invagination lies embedded. This portion of the neural crest later becomes divided into two lobes between which the auditory organ lies. In a still later stage the two lobes have become thinned out into sheets of mesoblast which extend one into the hyoid gill arch and the other into the first branchial gill arch. The seventh and ninth cranial nerves are probably also formed from the neural crest. The intimate relation of the auditory invagination to these lobes of the neural crest produces a striking resemblance to the condition found in the sensory anlage in teleosts. Here a single elongated thickening is described as dividing by two transverse fissures to form the anlage of the branchial sense organ, the auditory organ and the lateral line system respectively.

2. The auditory and lateral line organs of *Amia* do not have a common anlage. The auditory organ arises before the lateral line and independently of it as an invagination of the nervous layer of the ectoderm and forms later a closed vesicle.

3. The lateral line appears first in an embryo in which the auditory organ is a closed vesicle. The four primary lines (supra-orbital, infra-orbital, opercular-mandibular, and post-auditory) all arise independently of one another and of the auditory organ as thickenings of the nervous layer of the ectoderm and unite later to form a continuous system.

LITERATURE.

Allis, Edward Phelps, Junior.

'88 The Anatomy and Development of the Lateral Line System in Amia calva. Journ. Morph., II., 463–458, Pls. XXX.–XLII.

Wilson, H. V.

'91 The Embryology of the Sea Bass (Serranus atrarius). Bulletin U. S. Fish. Com. Washington., IX. (1889), 209–277, Pls. LXXXVIII.–CVII.

Wilson, H. V., and Mattock, J. E.

'97 The Lateral Sensory Anlage in the Salmon. Anatomischer Anzeiger, XIII., 658–660, two figures.

Mitrophanow, Paul.

'93 Étude Embryogénique sur les Selachiens. Archives de Zool. Exp. (3), I. 160–220, Pl. IX.–XIV.

Explanation of Plate I.

Fig. 1. Embryo of *Amia* in which there is a thickening (*th.*) of the mesectoderm or neural crest on the neural tube just back of the hind brain. × 20.

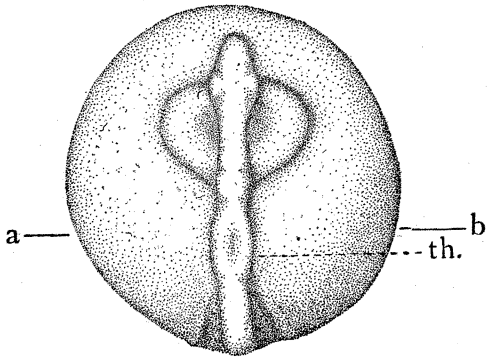
Fig. 2. Section through thickening along the line *a–b*, Fig. 1 showing neural crest and auditory invagination. *a.in.*, auditory invagination; *ec.*, ectoderm; *en.*, entoderm; *n.c.*, neural crest; *n.t.*, neural tube. × 167.

Fig. 3. Embryo of *Amia* showing the division of the thickening (*th.*) into two lobes. × 20.

Fig. 4. Section along the line *a–b*, Fig. 3, showing the gradual merging of the neural crest into the surrounding mesoblast. *ec.*, ectoderm; *en.*, entoderm; *n.c.*, neural crest; *n.t.*, neural tube. × 167.

Fig. 5. Embryo of *Amia* showing the extension of the neural crest into the spiracular and first branchial arches. *ad.org.*, adhesive organ; *a.p.*, auditory pit; *1st b.a.*, first branchial arch; *h.a.*, hyoid arch; *m.a.*, mandibular arch. × 20.

Fig. 6. Section through line *a–b*, Fig. 5, showing the constriction of the auditory invagination from ectoderm. *a.in.*, auditory invagination; *ec.*, ectoderm; *en.*, entoderm; *n.t.*, neural tube; *ntc.*, notochord. × 167.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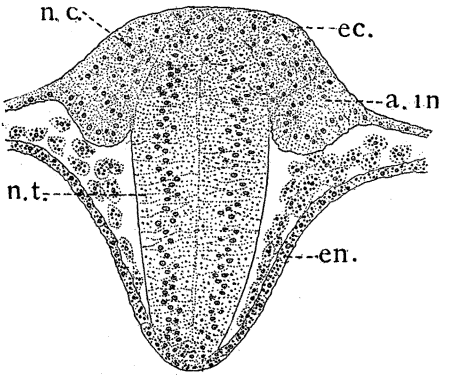
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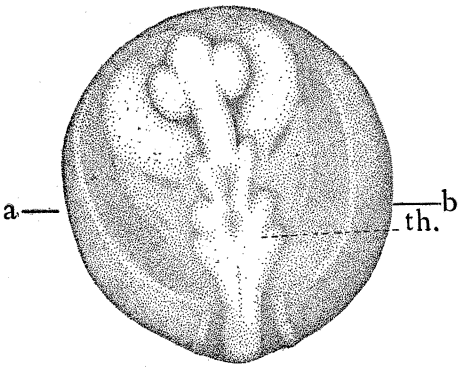
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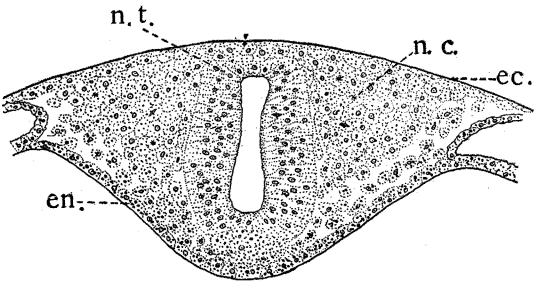
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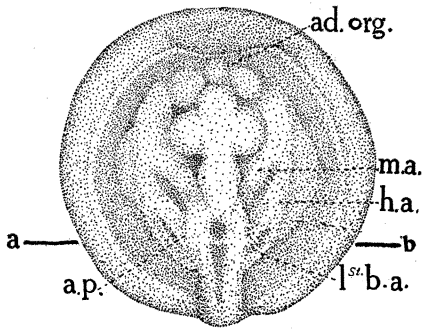
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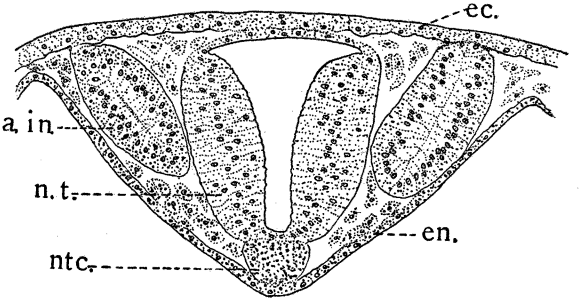
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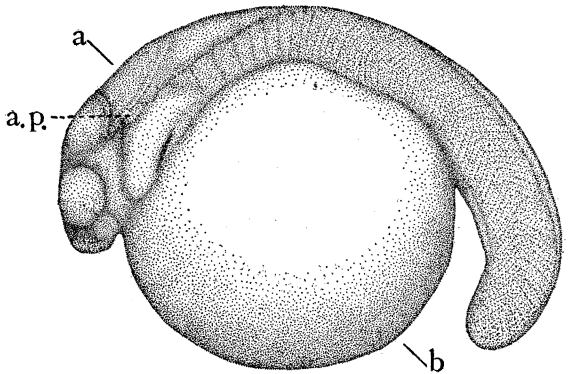
Explanation of Plate II.

Fig. 7. Embryo of *Amia* in which the lateral line anlage is first visible in section but not in surface view. *a.p.*, auditory pit. × 20.

Fig. 8. Section along line *a–b*, Fig. 7, showing the first appearance of the anlage of the lateral line. *ec.*, ectoderm; *ht.*, heart; *n.t.*, neural tube; *ntc.*, notochord; *p.a.l.l.*, post-auditory lateral line. × 167.

Fig. 9. Embryo of *Amia* showing the auditory pit. The lateral line anlage is visible as ridges, in both head and body regions. *a.p.*, auditory pit; *i.o.l.l.* infra-orbital lateral line; *o.m.l.l.*, opercular mandibular lateral line; *p.a.l.l.*, post-auditory lateral line; *s.o.l.l.*, supra-orbital lateral line. × 20.

Fig. 10. Section along line *a–b*, Fig. 9, showing the thickening of the inner layer of ectoderm to form head lines. *ec.*, ectoderm; *i.o.l.l.*, infra-orbital lateral line; *n.t.*, neural tube; *op.v.*, optic vesicle; *s.o.l.l.*, supra-orbital lateral line. × 167.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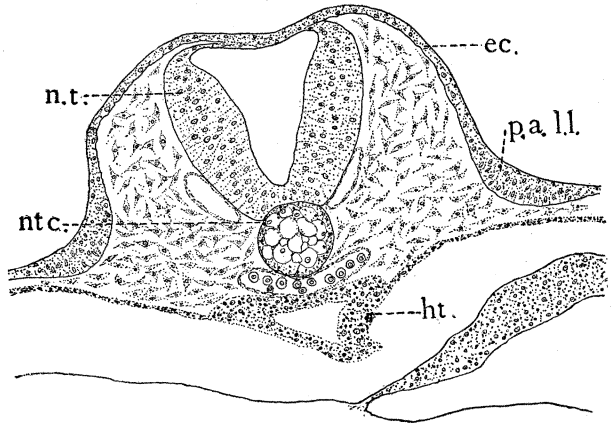
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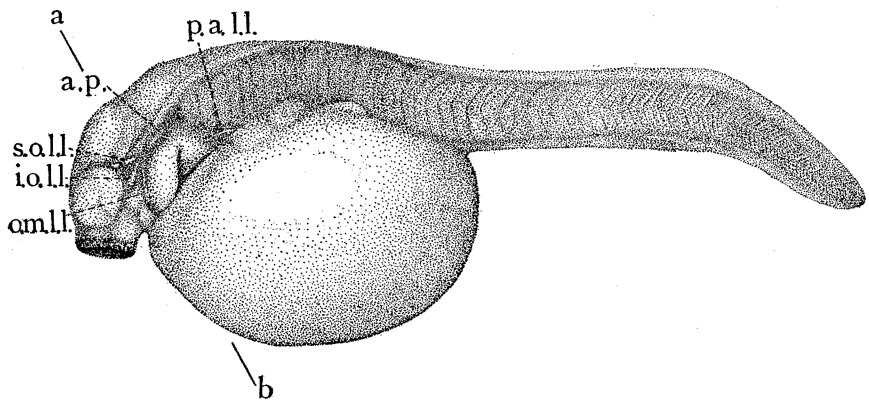
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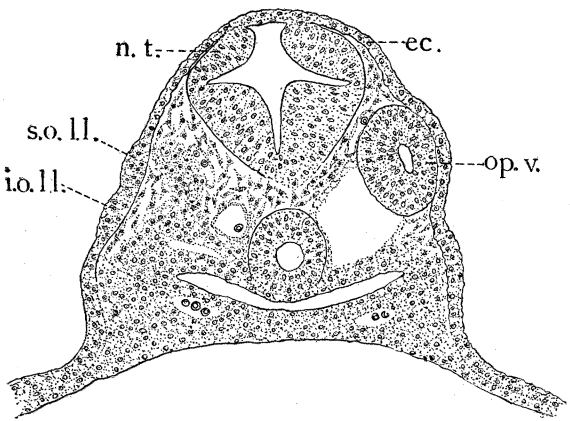
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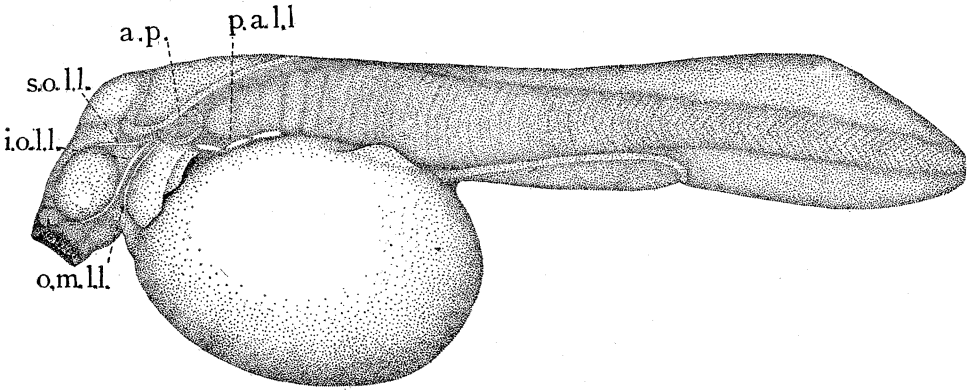
Explanation of Plate III.

Fig. 11. Embryo of *Amia*, newly hatched, showing further development of the four primary lateral lines. *a.p.*, auditory pit; *i.o.l.l.*, infra-orbital lateral line; *o.m.l.l.*, opercular-mandibular lateral line; *p.a.l.l.*, post-auditory lateral line; *s.o.l.l.*, supra-orbital lateral line. × 20.

Fig. 12. Embryo of *Amia*, one day after hatching, showing the four primary lateral lines before definite sense organs are differentiated. × 20. *a.p.*, auditory pit; *i.o.l.l.*, infra-orbital lateral line; *o.m.l.l.*, opercular mandibular lateral line; *p.a.l.l.*, post-auditory lateral line; *s.o.l.l.*, supra-orbital lateral line.



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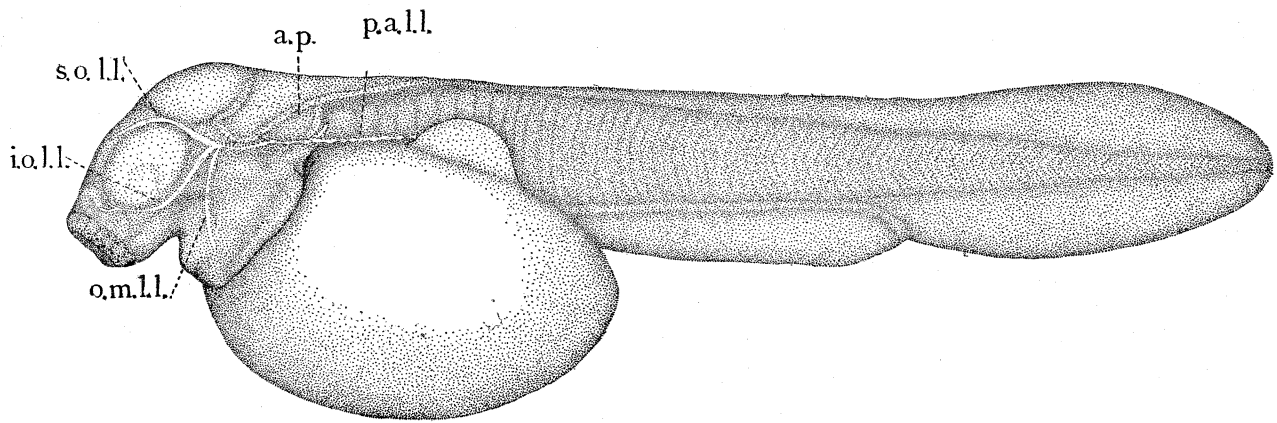

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